CHAPTER I.

Introduction.

The question about the morphological value of the ovule, has long been the subject of investigation and discussion, but a decisive answer is stil waited for. The first step to be done in order to throw light on this problem, is to determine to which category of organs, shoot, root or leaf, it can be classified as a whole. Especially during the nineteenth century there has been a good deal of disputing about this subject and nearly all morphologists have occupied themselves more or less with this question.

Finely their conceptions and opinions settled on three theories, which are to be mentioned later on, but nobody could give such convincing arguments, that one theory was accepted every where.

Gradually, however, the botanists have adopted the principal idea of one of those theories, and now-a-days it is generally granted, that the ovule is borne by a leaf, at least belongs to it, but a correct interpretation of the nature and the origin of both integuments and the nucellus is very little certain.

The investigations concerning the ovule started from the conditions of the Angiosperms and in order to state the nature of nucellus and integuments, five different methods were used, viz. the ontogeny, the anatomy, the topographical-morphology, the phylogeny and the teratology.

As to the ontogeny, this is often of very little importance for plants in general, as the organs after passing through a long phylogenetical development unfold immediately or grow into the now existing form, without repeating more or less their phylogeny, as is often the case in the animal kingdom. In most cases we see the origin of the ovule as a small papillate protrusion, around which both integuments originate and develop as annular walls in basipetal succession.

Though the ontogeny itself gives little occasion of research, so much the more several botanists made use of teratologicals. There is much difference of opinion about the value we may attach to such deviations and it occurs rather often that investigators are willing to take teratologicals into consideration, when they are useful in the authors argumentation, whereas they are rejected, when in contradiction to their statement. Therefore it is necessary to make a very cautious use of them, and we may only speak with certainty of retrogressive metamorphoses when deviations are found, clearly indicating a lower state of development as is already known in related plants, less far advanced in evolution. In this case they are of great importance and we owe many links of relation and origin to the observation of these teratologicals.

A great value was always attached to what we may call the topographical morphology, according to which an organ can be determined by the place where it occurs on the plant. To give an example, the ovules of the *Primulaceae*, which are borne on an axial placenta, are

sometimes said to belong to the shoot, whereas the parietal or marginal ovules, such as are found in the greater part of the other Angiosperms, are considered as parts of a leaf.

It is especially van Tieghem and his followers, who have treated the anatomical method, and recently also many English botanists attach a great value to the vascular-supply, and form their morphological conclusions accordingly. However constant the vascular-supply may be in many cases, we may not, as to my opinion, lose sight of the fact that these organs are always secondary, that a leaf does not originate for the sake of a vascular bundle, but that a vascular bundle has the function to supply the leaf. And though it may be possible that in many cases the remaining vascular bundles indicate the place of reduced organs they supplied, and thus can be used to sustain the other arguments, it is not allowed to make far-reaching conclusions from the vascular-supply alone.

Finely the phylogeny though acknowledged as being of great importance, has hardly been used by any of the former botanists. No one has treated the subject in comparing the same organs of the different divisions of the vegetable kingdom to its utmost consequence, which indeed was not possible in that time through lack of sufficient material. At most the results obtained by a comparison of the higher- with the lower-developed plants, were accepted as a proof of a once founded theory.

And yet this manner of research, sustained by the study of obvious retrogressive deviations, is the most certain mean to determine morphological values.

It is true that Čelakovsky takes the phylogeny into consideration but his views are wholly based on teratologicals and „Vergrünungsgeschichten" without accounting for wether these deviations are really retrogressive. Though he acknowledges (33) p. 169 the difficulty of

knowing for certain to which cause the deviations are to be attributed and which consequences may be concluded from, he starts entirely from the supposition that his „ovulum-antholysen" are „Rückschlagserscheinungen".

According to these methods of investigation, but chiefly by means of the three first ones, the three groups of opinions mentioned in the beginning were formed. Worsdell in his paper „On the structure and morphology of the ovule" (180) has given a review on these different theories, in which the ovule is said to have the value of a bud or of a leaf, or cannot be classified at all in one of those catagories, and which theories can be indicated for shortness' sake respectively as the axial, foliolar and sui-generis theory.

For a more detailed treatment I can refer to this excellent article of Worsdell, and I will confine myself to mention only the contents and the names of the followers of those views:

Axial theory.

The nucellus is of the nature of a bud and both integuments are its lateral foliar appendages St. Hilaire, Schleiden (129), Payer, Braun, Peyritsch, Pearson (113).

Foliolar theory.

The ovule belongs morphologically to the category of the phyllome; the nucellus is of the nature of an emergence, borne on the upper surface of a leaflet of the carpel, whereas the integuments are the fused lateral lobes of the same segment of the female sporophyll.

Brogniart (26), R. Brown (28), Caspary, Cramer (53), Prantl, Warming, Celakovský.

Sui Generis theory.

The ovule is an independent structure, borne either on cauline or foliar organs. The integuments are new formations around the nucelles.

Schmitz (130), Sachs (124), Strasburger (150), Goebel (68), Balfour.

As is proved by his treatment of this subject, Worsdell too is an upholder of the second theory, which is based for the greater part on the investigations of Čelakovský. The latter has adopted his opinions as to the foliar origin of the integuments, in consequence of a great number of the above mentioned Antholysen of ovules.

And really it is no wonder that, where he has found several cases (*Anagallis*, *Dictamnus*, *Alliaria*, *Hesperis*, *Trifolium* a.o.) in which both integuments are proliferated more or less and appear to be the fused lobes of a leaflet of the carpel, the nucellus originating on this lobe, like an emergence or like a sporange, it has become his conviction that both integuments are nothing but slips of the carpel: „Das verlaubte blattbürtige Eichen ist also ganz gewiss ein wirklicher Blatttheil, ein Fiederblättchen des Carpells, und da der morphologische Werth eines jeden der drei morphologischen Grundgebilde eines differenzirten Sprosses, nämlich des Kauloms, Phylloms und Epiblastems durch keine Metamorphose, also auch nicht durch die rückschreitende abgeändert werden kann, so ist auch das normale behüllte Eichen einem Carpellar-Fiederblättchen aequivalent" (33) p. 201.

The axial ovules of the *Primulaceae* too were proliferated and at the end of his article he says: „die behüllten Eichen sind immer und überall metamorphosirte Blattsprossungen oder Blattfiedern der Carpelle, entweder des Blattkörpers selbst (sogenannte blattbürtige Eichen) oder der Blattsohle (sogenannte axenbürtige Eichen): Selbständige Ovularblätter giebt es nicht."

„Aus diesem Satze folgt schon, dass die Hülle des Eikerns der Coniferen kein Integument sein kann, denn wäre sie

es, so müsste man nach dem zugehörigen Carpelle fragen, welches aber nicht vorhanden ist" p. 230 [1]).

And somewhat further: „Wir dürfen nunmehr ganz allgemein sagen, dass alle Eichen, behüllte und unbehüllte auf einem Fruchtblatte entspringen oder von ihm abhängig sind. Kein Eichen ohne Carpell" (p. 232). After having stated this axioma Čelakovský (40) tries to homologize the integument of the Angiosperms with the sporange-envelopments of the lower plants. In the first place he makes a comparison between the indusium of the ferns and the integument, and though it seems rather unjustifiable to connect in a direct way, a leaflet of a fern with a carpel from an ordinary flower, he yet says according to a comparison with a proliferated ovule of *Hesperis* „Somit ist auch der Blattzipfel eines Farnblattes, der das Indusium (den Schleier) auf seiner Unterseite trägt, das Äequivalent des äusseren Ovularinteguments von *Hesperis*" (p. 304).

His further papers, published on this subject, amount to this, that he wants to defend the theory he once put forth, and though he gives many sagacious proofs, the suppositions from which he starts are not quite certain, so that his method of investigation is the exact counterpart of what would be desirable in this case. For in stead of controling a same organ in its phylogenetical development from low to high, he first states the morphological value of nucellus and integument in their highest degree of development and then he puts the organs of lower plants aequivalent to them.

As I said already in the beginning it seems to me the weak point in Čelakovský's theory, that he has immediately assumed, that the proliferations of the Angiosperms would be retrogressive phenomena. Though lateron he begins to doubt this view and agrees with the possibility,

[1]) Lateron he is obliged to accept an integument in the Conifers.

that the proliferations could be progressive deviations, he doesnot change his opinions accordingly.

In this supposition his theory is not sufficiently established, for if this be true, a virescent condition can never throw light on the phylogenetical origin; a comparative investigation only can do this.

Now it is just in the latter half of the last century that new ways are opened for this comparative method by the discovery and accurate descriptions of fossil seeds. And almost independent of the discussed theories, which were founded for the greater part by German botanists, the question concerning the origin of the integument has been treated in England from a quite different point of view on account of discoveries such as *Lagenostoma Lomaxi, Trigonocarpus* a.o.

It is especially Miss Benson (15) who has given a quite new theory, being led to this in comparing the seed *Lagenostoma Lomaxi* with the microsporange *Telangium Scotti*, which is probably borne as well as *Lagenostoma* by *Lyginodendron Oldhamium*.

For the description of *Lagenostoma* I may refer to a following chapter of my paper, where the several seeds are described separately. Of *Telangium Scotti* I will cite here the diagnose given by Miss Benson herself (p. 162).

„Fertile and barren pinnae dissimilar; fertile pinnae represented by synangia only; synangia borne at the entremity of the ultimate ramifications of rachis, composed of 6—12 sporangia which taper to the apex and are united primarily for almost their whole length to form a body which is continued into a sterile base of decreasing diameter through which runs longitudinally a single vascular strand. Each sporange ultimately becomes almost free from the others by septicidal dehiscence and liberates large spores from a ventral suture."

Everyone, who compares both organs with one another,

will be struck by the resemblance in organisation of the synangium *Telangium* on the one hand and the seed on the other.

„The chambers surrounding the nucellus seem to represent its sister sporangia, which have become sterile, the large-celled, thin-walled tissue and delicate vascular strand being all that represents the ancestral sporogenous tissue; while the micropyle corresponds with the original space between the tips of the sporangia. The seed in fact is assumed to be a synangium in which all but one of the sporangia are sterile, and form an integument to the one fertile sporange which has become a megasporange with one large megaspore. In *Lagenostoma physoides* the integumental ridges are continued into tapering tentacles around the micropyle, and this still further accentuates the resemblance to a sorus" (p. 169). „Hence we have only to imagine that one of the sporangia of a sorus of eight or ten sporangia gradually evolved megaspory, and that the remaining seven or nine sporangia became a sterile envelope" (p. 169).

Here we have the whole so-called synangial-theory, which is based entirely on the undeniable resemblance between a synange and a seed, but which has this great disadvantage, that nothing of it is duely established and that the evidence of the facts is too meagre, to allow the drawing of such far reaching conclusions.

It occurs in several fern-sori, that some synangia remain sterile and are scattered amongst the others as paraphyses, but that the middle-one should always be fertile and the surrounding sporangia sterile, to form a closed outer envelopment, is quite unknown as a rule in any plant.

Oliver (104) therefore opposes this opinion of Miss Benson and regards the integument as being a new structure. He compares the fructifications of the Pteridosperms rather with those of *Lepidocarpon* and

Azolla, where an envelope occurs around the macrosporange as a new entirely independent annular covering.

„Though it may be premature to attempt to define in terms of stimulus and response the precise sequence of events that leads up to encasement, it will be readily admitted that a new departure such as the inception of the seed habit (where provision has to be made for the increased nutrive drain involved by the retention of the gametophyte) would be accompanied by nutrive disturbances that might easily favour the appearance of new formations" (p. 104).

Now that I have endeavoured to give some of the most important theories, concerning the origin and value of the integument, and to show how much these conceptions differ from one another, some questions are obvious viz.

1. The integuments of the Pteridosperms, Gymnosperms and Angiosperms are they comparable with one another, or is their origin polyphyletic.
2. If the integuments are homologous organs, are they also homologous with the indusium of the Ferns.
3. Is the integument composed of several units, which may be evident as ribs or sutures or as slips at the micropyle.
4. If the integument is composed of units, what is their value.

It is the intention of the present paper to try to solve these questions or at least to throw a new light on these problems. I shall therefore describe in the second chapter some of the most characteristic fructifications provided with an integument, attempting to mention the results of each investigation as objectively as possible, without falling into any subjective supposition.

Though in the descriptions of the palaeobotanical seeds no new observations are recalled, I have collected the data from the literature in the same order as the others, because they were not complete in any textbook.

In the third and last chapter, I will try to give a conclusion, based on a mutual comparison of these different seeds and ovules.

The material I used. I received partially from the Botanical Gardens of Lisbon, Rome and Buitenzorg, for which I desire to express my gratitude to the directors of those institutes. A thankful use I was enabled to make from a collection of dried seeds, present in the Botanical Laboratorium in Groningen.

Finely several specimens I could collect in the Hortus Botanicus of the fast mentioned University.